

Amphibian decline, pond loss and reduced population connectivity under agricultural intensification over a 38 year period

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Abstract Habitat loss, together with less obvious land-use changes such as intensified farming practice, can have significant adverse impacts on biodiversity. An important factor in determining the ability of species to cope with such changes is their potential to sustain a populations network by dispersal across the landscape. Habitat quality and structure are particularly important for surface-dwelling species with low dispersal abilities, such as amphibians. To assess this ecological function, ponds in a coastal and typically rural area of northern France were surveyed for amphibians in 1974, 1992 and 2011. These repeated surveys yielded different outcomes for different species groups. Three rare species persisted in more or less specialized habitat types. Two moderately common species declined, but kept strongholds in coastal dunes and associated marshes. Five common species with broad ecological niches remained equally widespread. The Northern crested newt declined markedly and the Midwife toad declined dramatically, as did their breeding habitats in vegetated ponds and cattle drinking troughs. One species, the Moor frog, may have gone locally extinct. A model of relative resistance to amphibian dispersal was created for different landscape types, on a scale from 0 (low resistance) to 1 (high resistance). This generated values of 0.23 for pasture, 0.72 for arable and 0.98 for urban and transport. As pasture declined in the study area, while arable and urban/transport infrastructure increased, amphibian dispersal became more difficult. However, dispersal paths proved difficult to evaluate in a patchy landscape like the one surveyed, due to a paucity of spatial

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signal. Pond loss is a more tractable reason for the observed amphibian species decline than is the quality of intervening terrestrial habitat matrix. In 2011, 22 newly created ponds had species richness in line with pre-existing ponds and this will have counteracted a dwindling metapopulation structure, indicating that habitat creation/restoration can play a valuable role in conservation. The colonization of new ponds may also prove more informative for gauging the potential for amphibian dispersal in the landscape than the preceding decline.

Keywords Dispersal · Graph models · Land use change · Least-cost models · Pond creation · Population persistence

Introduction

The second half of the twentieth century saw a major revolution in agricultural practice (Blaxter and Robertson 1995). The resulting increase of arable agriculture, over traditionally-managed mixed agriculture and pasture has caused widespread declines in farmland biodiversity (Benton et al. 2003; Tschardt et al. 2005; Reidsma et al. 2006). Together with parallel increases in urbanization and transport networks, these changes mean that landscapes rich in biodiversity have frequently been destroyed or lost the potential for harbouring wildlife. In particular, landscape modifications most affect those taxa that show a high reliance on specific terrestrial ecosystems and have low dispersal capability, such as amphibians. Moreover, this group of species relies on both aquatic and terrestrial environments, making them especially vulnerable to changes in both types of system (Stoate et al. 2009; Becker et al. 2010; Tryjanowski et al. 2011). As a result, it is widely regarded that habitat loss and alteration, largely due to ongoing changes in agricultural practice and wider land-use, has been the overarching factor causing declining amphibian populations in large parts of the Holarctic (Collins 2010; Heatwole 2013; Houlahan et al. 2000; Cushman 2006; Gardner et al. 2007; Trochet et al. 2014).

Linked to habitat area and quality, the persistence of populations within a landscape is also crucially determined by the ability of an organism to move through the environment (Beier et al. 2008). In metapopulations, the long-term viability of species is dependent on dispersal—which is the successful breeding of an individual in a place other than where it was born. Practical nature conservation has often been focussed on enhancing key breeding sites, but there is increasing awareness of the need for protection and restoration of habitat corridors and other components in the environment that promote dispersal (Sutcliffe et al. 2003; McRae et al. 2012). An animal group in which metapopulation structure may be especially pronounced is the Holarctic amphibians, including frogs, toads, newts and salamanders. Most species produce large numbers of offspring, mostly in stagnant water (i.e., ‘ponds’). After larval development and metamorphosis some of the juveniles will attempt to disperse (Cushman, 2006), a process which can take several years (Semlitsch, 2008). Their dispersal success will depend on both pond availability (i.e. quantity—the distance to travel) and on the characteristics of the intervening landscape (i.e. quality—the difficulty and risk of travel) (Marsh and Trenham 2001; Mazerolle and Desrochers 2005). Models for population connectivity have to consider both factors as well as their interaction but, as yet, few studies have addressed their relative importance (for an amphibian example see Fortuna et al. 2006).

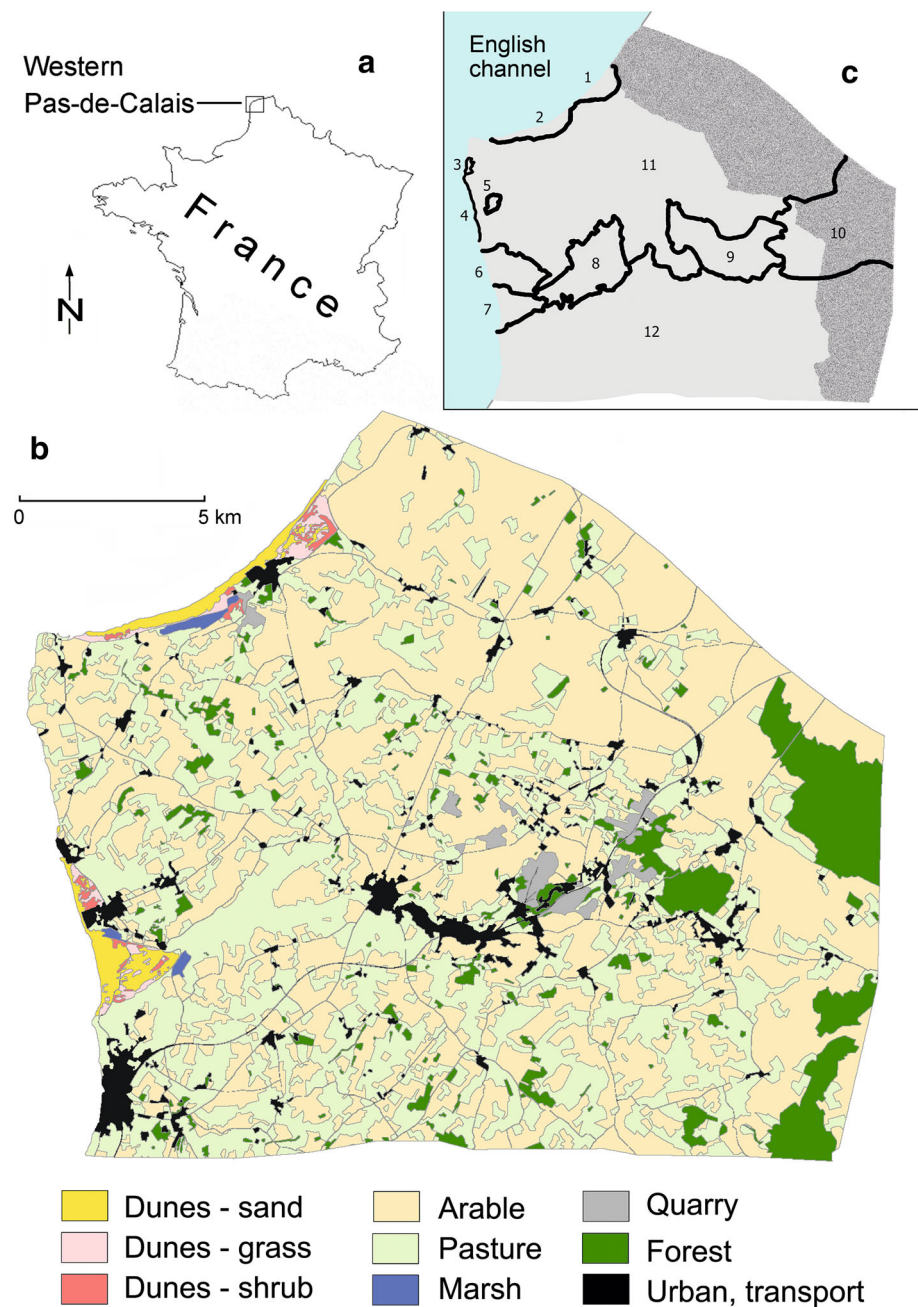
Animal dispersal over the landscape has two components: functional connectivity, which depends on the behaviour of a dispersing organism within the landscape, and structural connectivity, which depends on the landscape spatial scale and configuration (Keitt et al. 1997; Baguette and Van Dyck 2007). In parallel to this, dispersal can be ‘informed’ or ‘naïve’. In the informed mode, decisions are made by an individual of a highly cognitive species (such as a bear, cougar or lion), which has the capability to locally select a route that minimizes the cost for movement (Chetkiewicz and Boyce 2009; Elliot et al. 2014). The alternative naïve mode is frequently applied in the context of metapopulation models, to more-or-less randomly moving individuals that rely on chance to make it through dispersal journeys (Bergerot et al. 2013). A combination of both strategies will probably apply to many organisms, in particular to terrestrial organisms with low dispersal capabilities such as amphibians (Brown et al. 2014; Campbell Grant et al. 2010). They will, on one hand, not be able to oversee longer routes, such as pond to pond dispersals, but may make well-informed decisions on the basis of the local environment they find themselves in. As data on individual paths are rare for amphibians and may refer to migration rather than dispersal, it is not possible to confirm whether dispersal routes are informed or naïve (Mazerolle and Vos 2006; Vos et al. 2007; Sinsch et al. 2012; Sinsch 2014). As a consequence, it is necessary to explore both options (Decout et al. 2012).

Animal dispersal can be regarded as a key determinant of breeding habitat occupancy. This approach recognises that landscapes are made up of habitat patches of varying quality, often with defined locations of high quality or importance (such as amphibian breeding sites) lying within a lower quality matrix. The permeability of this matrix has a critical role in determining community structure and population dynamics through its effects on dispersal and colonization between high quality locations (Donald and Evans 2006). Evidence for this has been found for a range of taxa, including amphibians (Gray et al. 2004). Declines in the quality of the landscape matrix reduce the ability of animals to travel the necessary distances between good habitat patches, increasing the chances of local population extinction. However, active landscape restoration can enhance connectivity and do much to help conserve vulnerable species.

We surveyed the coastal area of the département (dpt.) Pas-de-Calais in northern France for amphibians in three surveys conducted in the last four decades. The particular aims of this were: (i) to document species assemblages and see how these are associated with land use; (ii) to see if and how these configurations have changed over time; (iii) to investigate how connectivity of amphibian populations has changed as a function of the loss of ponds and change in land use, and (iv) to analyse how the creation of new ponds for amphibians may help to counter the fragmentation of populations. The dpt. Pas-de-Calais represents very well the post-war intensification of agriculture and the increase of built infrastructure, yet some areas including the coastal dunes and associated wetlands are largely unaffected and serve as a useful reference. As a result, the taxa chosen and the study area are suitable to illustrate how landscape change can affect habitat occupancy, connectivity and metapopulation structure through its impacts on dispersal.

Materials and methods

The study area covers ca. 300 km² of the western part of the dpt. Pas-de-Calais (Fig. 1) and falls almost entirely under the ‘Parc Naturel Régional des Caps et Marais d’Opale’. The landscape is dominated by agriculture, with both pasture and arable land present. Along the



coast, two large dune areas are found, with associated wetlands, while substantial areas inland are covered by forests and quarries. The study area was divided into 12 geographical sections based upon a past (1963, Fig. 1) and more recent (2003, Appendix I in Supplementary materials) land-cover classification (Curado et al. 2011).

Fig. 1 Study area in the coastal zone of the dpt. Pas-de-Calais, France surveyed for the presence of amphibian species in 1974–1975, 1992 and 2011–2012, with **a** position within France and **b** land use in 1963, redrawn from Curado et al. (2011). For land use in 2003 see Appendix I in Supplementary materials. **c** Land use defined sections within the study area are: 1 Dunes d’Amont, 2 Dunes d’Aval and dunes du Chatelet, 3 Bomb crater pasture area, 4 Cliffs, 5 ‘Museum’ terrain, 6 Selles brook and communal pasture, 7 Dunes de la Slack, 8 Valley of the Slack, 9 Quarry area, 10 Inland forested area, 11 Northern agricultural land and 12 Southern agricultural land. Several large scale arable and forested areas in the north and the east were visited irregularly and are outside the core of the study area (outer area, shaded)

The area was first surveyed for amphibians in the spring and early summer of 1974 (AZ, together with H. Hooghiemstra) and 1975 (JWA, together with A. G. M. Gerats), for a second time in spring 1992 (CA, with assistance of JWA and AZ) and for the third time in spring and early summer 2011 (WRMM and AZ) and in the spring of 2012 (JWA). Potential amphibian breeding sites were located in the field visually, aided by 1:25,000 topographical maps of the ‘Institute Géographique National’ and through contact with local naturalists and employees of the Parc Naturel Régional. Pond coordinates were taken from IGN maps (first survey) or by GPS. Surveys were undertaken during the main amphibian breeding period and were commonly repeated through the season to limit seasonal constraints. We distinguished nine pond types in the field, based upon their origin and levels of aquatic vegetation (e.g., various types of field ponds and cattle drinking troughs; see Appendix II in Supplementary materials).

A typical site visit to each pond included a search for amphibian eggs and embryos, dip netting for larvae and aquatic adults and a search of the terrestrial habitat in the vicinity. Evening and nightly visits were made to find amphibians by torching (mostly adults) and to detect anuran species from their mating call. Species identification was unproblematic except for the eggs, embryos and larvae of the two *Lissotriton* species (*L. helveticus* and *L. vulgaris*). This limitation will have affected the overall results for detecting presence/absence only marginally, since *Lissotriton* adults are often abundant and unproblematic to observe. Single observations and count data in the field were recoded as presence/absence data for each pond.

We recognized three classes of species prevalence, namely: (i) common species—observed in >25% of the ponds, (ii) species of moderate occurrence—observed in $\geq 10\%$ and $\leq 25\%$ of the ponds, and (iii) rare species—observed in <10% of the ponds. We distinguished between ‘single survey ponds’ and ‘persisting ponds’. Single survey ponds are those that: (i) figured in the first survey but had disappeared or were without amphibians in the third survey, or (ii) figured in the third survey but were missed or without amphibians in the first survey, or had been newly created. This latter category included 22 field ponds restored or created by the Parc Naturel Régional (J. Robilliard, pers.comm., April 2011). Persisting ponds are those that were present and with amphibians at both the first and third survey. Information on pond presence from 1992 was not used within this classification due to the conditions of drought over the preceding 1991–1992 winter, so that many ponds present at the first and third survey did not hold water and were unavailable for amphibian reproduction.

On average, ponds were visited most often in the first survey (average 3.0 visits, range 1–5), compared to the second (average 2.0, range 1–7) and third surveys (average 2.5, range 1–4). Within the first survey the number of visits was higher for species-rich ponds than for species-poor ponds (for data see Appendix II in Supplementary materials), constituting a potential bias to the surveying results. However, more visits to many ponds were often made with additional interests in mind, such as phenology, larval growth and metamorphosis, breeding behaviour and inter-species relationships. As a result, we

consider that, in effect, the surveys have been representative in terms of species search effort per locality and that the species presence/absence data for each pond is accurate. We were frequently denied access over parts of landscape Sections 1, 2 and 9. In addition, initial visits showed that several large-scale arable and forested areas in the north and the east turned out to be poor in waterbodies and amphibians, and these were visited infrequently.

To determine how the terrestrial habitat around ponds influenced the presence of amphibian species using them, land-use data were extracted from published maps for a 200 m radius around each pond (Curado et al. 2011). This radius was chosen as a compromise between mapping accuracy, average inter-pond distance in the study area and the distance that adult amphibians reside, migrate or disperse from ponds (Semlitsch and Bodie 2003; Smith and Green 2005; Trochet et al. 2014). Land use data were also extracted over hypothesized inter-pond dispersal routes (see below). The dates for the environmental maps precede the biological data gathering by about a decade. We consider this appropriate for our study because of the observed time-lag between agriculture-mediated habitat loss and the impact this has on population persistence (Löfvenhaft et al. 2004; Piha et al. 2007). Ten land-use classes were distinguished: arable, dunes-sand, dunes-grass, dunes-shrub, forest, marsh, pasture, quarry, transport and urban. Upon analysis, the three dune classes were grouped together (dunes), as were transport and urban (TU). GIS analyses were carried out with ILWIS 3.3 (ILWIS 2005) and statistical analyses were done with SPSS 20 (IBM Corp. 2011).

Associations of amphibian species occurrences, land-use and pond type were estimated with a Canonical Correspondence Analysis (CCA) in Canoco 5 (Šmilauer and Lepš 2014) under settings suggested by the software. Land-use data were calculated as arcsine transformed fractions (number of pixels representing land-use class/number of pixels considered). Pond types were binary coded and rare species were downweighted. The survey results, along with the CCA classification, indicated a sharp decline in drinking trough and vegetated pond habitats, which typically support the presence of *Alytes obstetricans* and *Triturus cristatus*. This led us to search for a concomitant decline in the potential for dispersal for these two species in particular.

To analyse landscape-derived resistance to amphibian dispersal we worked under the assumption that good habitat to live in is good habitat to disperse through (Mateo-Sánchez et al. 2015; see Zeller et al. 2012 for a general discussion). We associated the presence of declining species with the widespread landscape features arable, pasture and TU of the first survey in a weighted logistic regression analysis. This indicated a positive association of declining species with pasture and negative associations with arable and TU. Accordingly, dispersal cost models were built with low landscape resistance values for pasture and high values for arable and TU. With this approach we largely avoided the use of ‘expert knowledge’ (Compton et al. 2007) for which results may be ambiguous (Charney 2012; Janin et al. 2009), or may generate false positive assessments.

For ease of analysis, the very large number of potential dispersal paths that might be taken by a naïve disperser were summarized as Euclidian distances between occupied ponds. These abstracted semi-random walks we call ‘links’. In order not to saturate the landscape maps with potential dispersal paths and to reduce spatial autocorrelation, only links were considered that make up a so-called ‘Gabriel network’. This is a type of network that reduces the many possible connections between nearby points in space while still demonstrating connectivity in a meaningful way. Gabriel networks were determined with Passage 2.0 software (Rosenberg and Anderson 2011). The dispersal path of an informed disperser, which we term as a ‘corridor’, was calculated with a least-cost algorithm in

Linkage Mapper (McRae and Kavanagh 2011). Only corridors corresponding to matching links in the Gabriel network were considered in our analysis.

Results

Amphibian species presence and decline

We recorded 13 amphibian species in the first survey, 11 in the second survey, and 12 at the third survey (Appendix II in Supplementary materials). The observations for the first and third survey are plotted in Appendix III in Supplementary materials. *Rana arvalis* was only observed at the first survey and the rarely recorded *Pelophylax kl. esculentus* was not identified in the second survey. Waterbodies with one or more potentially breeding amphibian species present ('ponds') were found $N = 209$ times in the first survey, $N = 95$ in the second survey and $N = 189$ in the third survey. The average number of amphibian species per pond was 3.7 (range 1–10) in the first survey, 2.9 (range 1–8) in the second survey and 3.0 (range 1–9) in the third survey. In the single survey ponds, the average species number went down significantly from 3.8 (range 1–10, $N = 163$) in the first survey to 3.0 (range 1–9, $N = 143$) in the third survey (Mann–Whitney U -test, $U = 9148$, $Z = -3.17$, $P < 0.01$). In 46 persisting ponds, the average species number went down from 3.5 (range 1–8) to 3.0 (range 1–7), this difference being statistically significant (Wilcoxon matched pairs test, $W = 159.5$, $Z = -2.16$, $P < 0.05$). The 22 newly created field ponds studied at the third survey had 3.6 species (range 2–7) and another 57 older field ponds had 3.2 species (range 1–6; Appendix II in Supplementary materials). This difference is not statistically significant (Mann–Whitney U -test, $U = 535.5$, $Z = -1.00$, $P > 0.05$).

The proportion of occupied ponds did not change significantly for five species between surveys (Table 1, panel A). However, the proportion of occupied ponds declined significantly for six species (*A. obstetricans*, *Epidalea calamita*, *Hyla arborea*, *L. vulgaris*, *Rana temporaria* and *T. cristatus*) and increased for one species (*Salamandra salamandra*). For persisting ponds, no significant change in the proportion occupied was noted, except for a strong decline in *A. obstetricans* from 33% to 8% of ponds being occupied (Table 1, panel B). When panels A and B of Table 1 were compared, the proportion of occupied ponds was not significantly different for any species, except for *H. arborea* that, at the third survey, was more frequent in persisting ponds than in single survey ponds (Table 1, panel C).

Partitioned over the 12 landscape sections, the proportion of occupied ponds declined for *A. obstetricans* in four sections and for *T. cristatus* in three sections, with mostly highly significant signals (Table 2). Four species (*E. calamita*, *H. arborea*, *L. vulgaris* and *R. temporaria*) declined in one or two sections, with modest statistical support ($P < 0.05$). Two species (*Bufo bufo* and *L. vulgaris*) increased in one section, also with modest statistical support. Ignoring the data points for which statistical support is modest, a decline stands out of *A. obstetricans* and *T. cristatus* in the landscape Sections 5, 9 and 11.

Community analysis

The Canonical Correspondence Analysis (CCA) revealed three species-environment assemblages in the first survey data. First is a group with the common anuran species *B. bufo* and *R. temporaria* typical of marshes, ponds with poor aquatic vegetation (*B. bufo*)

Table 1 The presence of 13 amphibian species in ponds over the study area in Pas de Calais, France, recorded for the first survey (1974–1975) and the third survey (2011–2012)

Species	A—ponds at a single survey (%)			B—persisting ponds (%)			C—G values for comparison A–B	
	First survey	Third survey	G	First survey	Third survey	G	First survey	Third survey
<i>A. obstetricans</i>	53 (32.7)	12 (8.4)	28.76***	15 (31.9)	3 (6.4)	10.64**	0.01	0.20
<i>B. bufo</i>	98 (60.5)	96 (67.1)	<u>1.45</u>	28 (59.6)	30 (63.8)	<u>0.18</u>	0.01	0.17
<i>E. calamita</i>	24 (14.8)	8 (5.6)	7.22**	7 (14.9)	7 (14.9)	0.00	0.00	3.71
<i>H. arborea</i>	23 (14.2)	8 (5.6)	6.45*	12 (25.5)	14 (29.8)	<u>0.21</u>	3.10	17.28***
<i>I. alpestris</i>	90 (55.6)	71 (49.7)	1.06	24 (51.1)	21 (44.7)	0.38	0.30	0.35
<i>L. helveticus</i>	88 (54.3)	71 (49.7)	0.66	19 (40.4)	19 (40.4)	0.00	2.83	1.21
<i>L. vulgaris</i>	60 (37.0)	37 (25.9)	4.40*	13 (27.7)	12 (25.5)	0.05	1.45	0.00
<i>P. kl. esculentus</i>	1 (0.6)	2 (1.4)	<u>0.48</u>	0	0	n.a.	n.a.	n.a.
<i>P. punctatus</i>	4 (2.5)	6 (4.2)	<u>0.71</u>	0	0	n.a.	n.a.	n.a.
<i>R. arvalis</i>	4 (2.5)	0	n.a.	0	0	n.a.	n.a.	n.a.
<i>R. temporaria</i>	92 (56.8)	65 (45.5)	3.91*	28 (59.6)	22 (46.8)	1.54	0.12	0.03
<i>S. salamandra</i>	5 (3.1)	12 (8.4)	<u>4.14*</u>	3 (6.4)	1 (2.1)	1.09	0.96	2.71
<i>T. cristatus</i>	45 (27.8)	19 (13.3)	9.89**	12 (25.5)	7 (14.9)	1.66	0.09	0.08

A distinction is made for ponds included on one occasion (i.e., either the first or the third survey, panel A with N = 163, resp. N = 143) and ponds that were studied at both surveys (panel B, N = 46). Statistical evaluation is by the G-test for goodness-of-fit (panels A and B) and by the G-test for independence (* P < 0.05, ** P < 0.01, *** P < 0.001, n.a.—test not applied). Underlined G-values indicate an increase in proportion occupied over time

and shallow ponds (*R. temporaria*), together in the top part of the CCA plot (Fig. 2a). Loosely associated to this group are *P. kl. esculentus* at inland pasture and *R. arvalis* at marshes. The second assemblage is a group with the five salamander species, along with *A. obstetricans*, extending over the lower left section of the CCA plot. These species are typically associated with a variety of terrestrial and aquatic habitats. For the two species which later undergo a strong decline, namely *A. obstetricans* and *T. cristatus*, the associated land-use types are quarries, TU, and moderately vegetated ponds. The drinking trough pond type is found to support *Ichthyosaura alpestris* and *L. vulgaris*, while arable and forest land-uses are associated with *S. salamandra* and *L. helveticus*. The third group, consisting of the anuran species *E. calamita*, *H. arborea* and *Pelodytes punctatus*, is typically associated with the dunes and to a lesser extent with marsh and quarries. In the CCA for the third survey *S. salamandra* associates with streams. The dune and marsh species are now joined by *A. obstetricans*, *T. cristatus* (Fig. 2b) and by *L. vulgaris*, which declined from the second to the third survey (Appendix II in Supplementary materials).

Population networks

Gabriel networks for locations of *A. obstetricans* and *T. cristatus* are shown in Fig. 3. The decline in observed pond use translates to a lower number of inter-pond connections. For 46 persisting ponds, the network appears denser in the southern agricultural area and along the coast than in the northern agricultural area (Fig. 3e), while the creation of new ponds

Table 2 Statistical evaluation of the number of occupied ponds in the study area in dpt. Pas-de-Calais, France from the first to the third survey per landscape section

Landscape section	1	2	3	4	5	6	7	8	9	10	11	12
Number of ponds												
First survey	3	11	2	1	25	28	27	23	9	2	46	32
Third survey	4	5	9	10	9	15	19	20	11	7	53	28
Species—vernacular name—species code												
<i>Alytes obstetricans</i> —midwife toad—Ao					**		*		**		***	
<i>Bufo bufo</i> —common toad—Bb												[*]
<i>Epidalea calamita</i> —Natterjack—Ec							*					
<i>Hyla arborea</i> —Tree Frog—Ha											*	
<i>Ichthyosaura alpestris</i> —Alpine Newt—Ia												
<i>Lissotriton helveticus</i> —Palmate Newt—Lh												
<i>Lissotriton vulgaris</i> —Smooth Newt—Lv							[*]				*	
<i>Pelophylax kl. esculentus</i> —Edible Frog—Pe												
<i>Pelodytes punctatus</i> —Parsley Frog—Pp												
<i>Rana arvalis</i> —Moor Frog—Ra												
<i>Rana temporaria</i> —Common Frog—Rt			*	*								
<i>Salamandra salamandra</i> —Fire Salamander—Ss												
<i>Triturus cristatus</i> —Northern Crested Newt—Tc					***				**		***	

Filled cells denote a significant increase (square bracket cells) or decrease (open cells) in proportion occupied (Fisher's exact test, * $P < 0.05$, ** $P < 0.01$ and *** $P < 0.001$). For empty cells, results are either not significant ($P > 0.05$) or no test was carried out for paucity of data

helped to restore the coverage of the pond network (Fig. 3f). For examples of population and pond loss see Appendices IV, V and VI in Supplementary materials.

Changes in land use

The most prominent change in land use in the study area has been the loss of pasture land, of between 7 and 22% in measured areas (Fig. 4, see also Fig. 1 and Appendix I in Supplementary materials). A local trend is apparent with a more prominent decline in the southern agricultural land (Section 12) than in the north (Section 11). Pasture loss is marginally higher around rather than in between breeding ponds and for persisting ponds compared to ponds with declining species. The loss of pasture is, to some degree, offset by an increase of pasture elsewhere, but we have no information on its impact on amphibian wildlife. Presumably modern hay meadows with no ponds are less favourable than traditional cattle pastures with ponds.

The logistic regression analysis yielded a significant association between the presence/absence of *A. obstetricans* and *T. cristatus* with the widespread land-use classes of arable, pasture and TU. The result is $P_o = (1/(1 + \exp*(1.158*\text{arable} - 1.006*\text{pasture} + 3.866*\text{TU} + 0.0*[\text{other land use classes}] - 0.194)))$, in which P_o is the probability of occurrence of *A. obstetricans*, *T. cristatus*, or both. The fit of the model is Cohen's kappa 0.62 which qualifies as 'good' (Altman 1991). The analyses were repeated for the variables

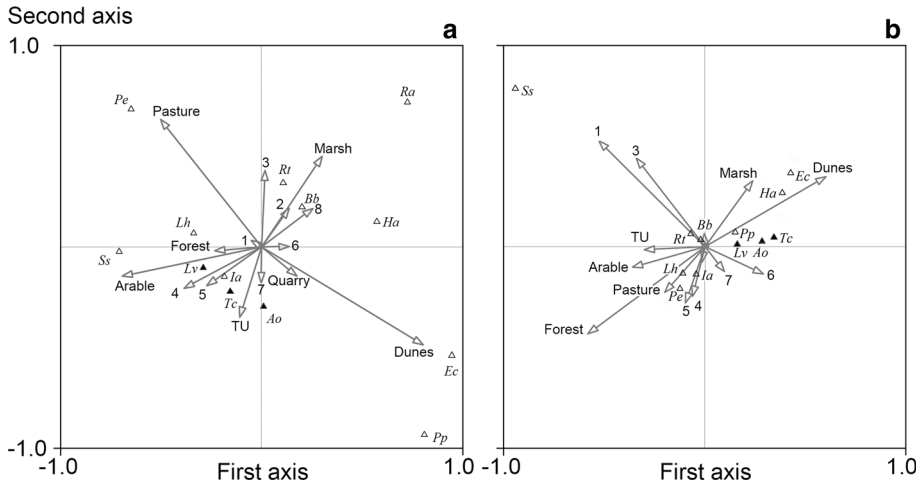


Fig. 2 Species–habitat associations for the amphibian fauna of dpt. Pas-de-Calais in north-western France estimated with Canonical Correspondence Analysis. **a** first survey, **b** third survey. Numbers refer to pond types (see Appendix II in Supplementary materials). For species codes see Table 2. Note that three species shown by solid triangles (Ao *Alytes obstetricans*; Lv *Lissotriton vulgaris* and Tc *Triturus cristatus*) are associated with pond types 4, 5 and 7 (drinking troughs and vegetated ponds) in the first survey and are associated with well-vegetated ponds (pond type 6) and dune areas at the third survey

individually, showing that the variable TU is not by itself significant ($P = 0.219$), arable is marginally significant ($P = 0.057$) and pasture is significant ($P = 0.033$). The land use resistance values following from these formulae are 0.72 for arable, 0.23 for pasture, 0.98 for TU and 0.45 for the other land use classes in combination. We accept the model as relevant because it makes biological and intuitive sense. The suitability of the terrestrial habitat around occupied ponds, shown by low values in Fig. 5, was better for *A. obstetricans* and *T. cristatus* and for the set of persisting ponds than for the study area as a whole. General habitat suitability increases in order Outer area to Northern agricultural land (Section 11) to Southern agricultural land (Section 12) (Figs. 1, 5). Not surprisingly, this is also the order at which ponds and pasture are being lost.

Potential for amphibian dispersal

The dispersal paths expressed as corridors are largely projected over pasture and, although their lengths in km are longer than the lengths of corresponding links, the resistance encountered is less (Table 3). The average resistance by the landscape over the hypothesized dispersal trajectories, calculated as either links or as corridors, has significantly increased for persisting ponds from the first to the third survey (Table 3). For ponds with *T. cristatus*, however, this effect is not significant and for *A. obstetricans* it is modestly (links) or marginally significant (corridors).

In the landscape here studied, in which the habitats are patchy and have a small grain relative to inter-pond distances (Fig. 1, Appendices I and III in Supplementary materials), the dispersal route chosen by the informed dispersal mode is not that much different from the path that summarizes the naïve dispersal mode. We illustrate this with an extreme example in which the elongated shape of the Marquise—Rinxent agglomeration (TU, with high resistance) does not much affect the calculated connectivity of *A. obstetricans* and

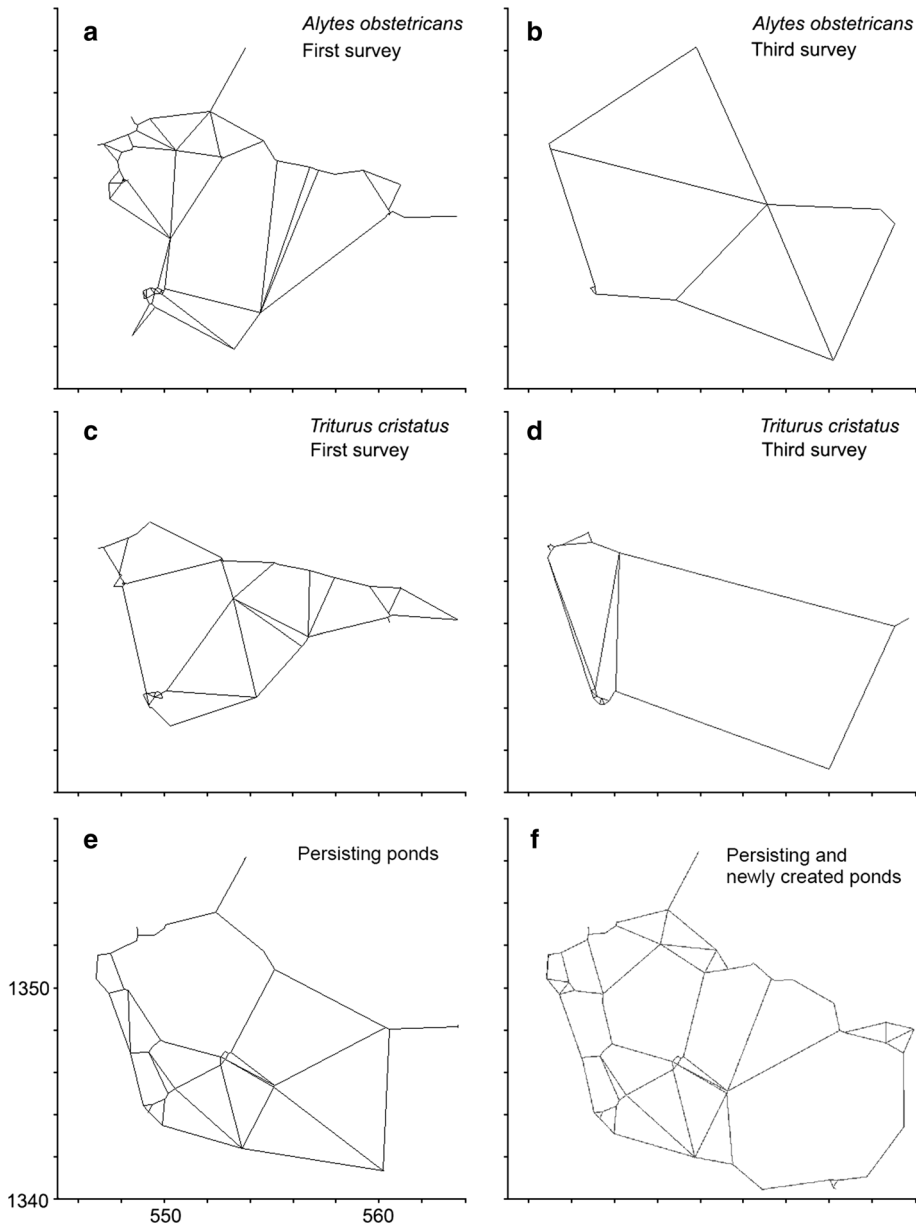


Fig. 3 Links for inter-pond amphibian dispersal in the study area of dpt. Pas-de-Calais, France. *Top panel*—*Alytes obstetricans* (ab) and *middle panel*—*Triturus cristatus* (cd). The *left* shows the situation for the first survey and at the *right* for the third survey. Only links are shown that together represent a Gabriel networks for occupied ponds. Panel e—as above, for ponds persisting from the first to the third survey, irrespective of amphibian species observed. Panel f—as e, plus third survey ponds newly created. Coordinates follow the Lambert I system

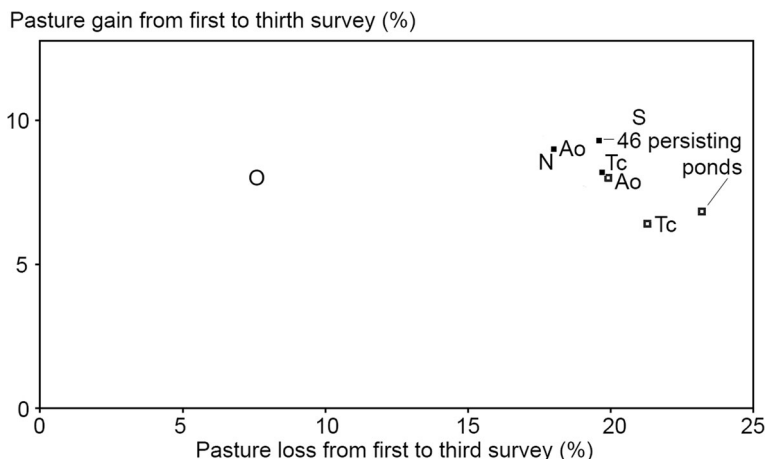


Fig. 4 Pasture land-use dynamics in the coastal zone of dpt. Pas-de-Calais, France from the first to the third amphibian survey. The magnitude of pasture loss (*horizontal axis*) and pasture gain (*vertical axis*) is shown by *capital letters* for three landscape sections of the study area (*N* northern agricultural land, *O* outer area and *S* southern agricultural land; for landscape sections see Fig. 1b), for species (*Ao*—*Alytes obstetricans* and *Tc*—*Triturus cristatus*) and for amphibians in general over 46 persisting ponds. A distinction is made between pasture land-use dynamics in between ponds (*solid symbols*) and directly surrounding ponds (*open symbols*)

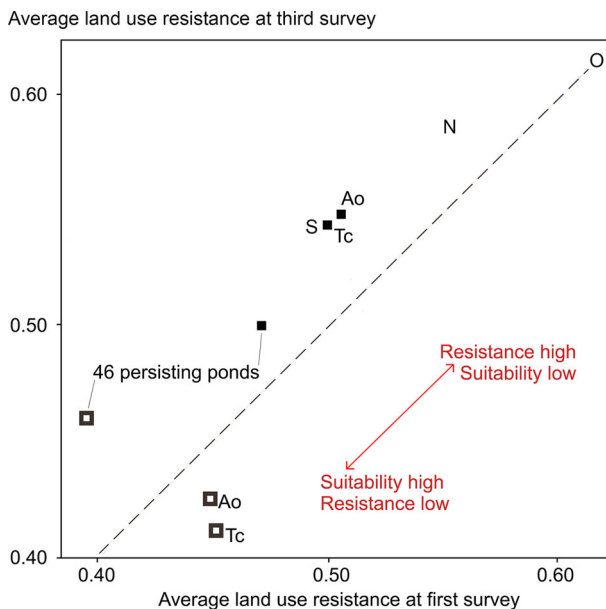


Fig. 5 Average resistance values to amphibian dispersal for the Northern agricultural land (*N*), the Southern agricultural land (*S*) and for the amphibian poor Outer area (*O*), for the first survey (*horizontal axis*) and the third survey (*vertical axis*). Average resistance around ponds (*open symbols*) and in between ponds (*solid symbols*) are shown for the species *Alytes obstetricans* (*Ao*) and *Triturus cristatus* (*Tc*) and for amphibians in general over 46 persisting ponds. Note that in our models habitat suitability and resistance are ‘two sides of one coin’, because of the underlying assumption that good habitat to live in is also good habitat to disperse through

Table 3 Average resistance imposed by the landscape over hypothesized dispersal trajectories at the first (1974) and third survey (2011) of amphibians in dpt. Pas-de-Calais, France

Pond type and species	Survey	N	Links			Corridors [#]		Correlation
			% Pasture	Resistance	Figure	% Pasture	Resistance	
<i>Alytes obstetricans</i>	First	36	38.8	0.472	3a	71.9	0.284	0.56***
	Third	10	24.7	0.552	3b	68.6	0.331	0.67*
	T test			*			(*)	
<i>Triturus cristatus</i>	First	26	40.6	0.504	3c	83.8	0.295	0.37(*)
	Third	10	26.2	0.547	3d	76.1	0.323	0.80**
	T test			NS			NS	
46 Persisting ponds	First	27	42.8	0.483	3e	83.6	0.297	0.63***
	Third	27	33.1	0.529	3e	45.6	0.465	0.60***
	Paired t test			**			***	

Ponds and populations considered form a Gabriel network and are separated by 1000 m or more

NS not significant

(*)— $0.05 < P < 0.10$, * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$

[#] For an example of corridors see Fig. 6

T. cristatus populations to the north and south (Fig. 6). The generality of this effect is shown by the significant correlation between the resistance to dispersal of links versus corridors (Table 3).

Discussion

A commonly occurring land-use change adversely affecting dispersal and population presence is the conversion of pasture into arable fields, along with the consequent loss of cattle ponds that amphibians use for breeding (e.g., Nyström et al. 2007; Piha et al. 2007; Janin et al. 2009; Curado et al. 2011; Hartel and von Wehrden 2013). We here studied the dpt. Pas-de-Calais which is among the most intensive agricultural production centres of France (Bas et al. 2009). We documented the persistence of, and connectivity among, amphibian populations as a function of the loss of aquatic and terrestrial habitats but declines in species richness have been reported for other (e.g., floral) groups also (Van Calster et al. 2008; Fried et al. 2009).

Species accounts and population developments

Common species

Bufo bufo was the most frequently observed species in all three surveys and was encountered in all 12 land use sections and in a wide variety of pond types (Appendix I in Supplementary materials). The newts *I. alpestris* and *L. helveticus* were and remained widely distributed throughout all surveys. *Lissotriton vulgaris* declined in the agricultural

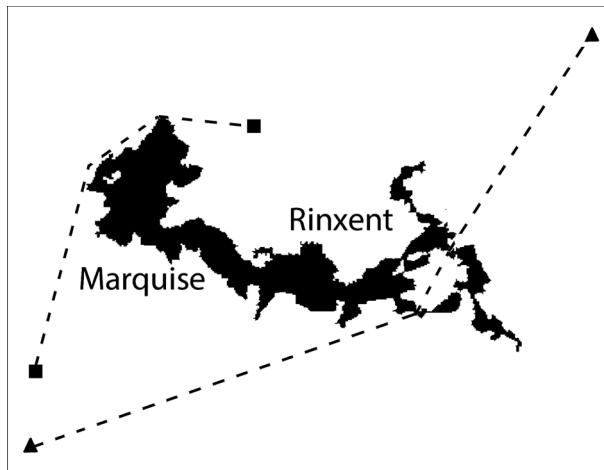


Fig. 6 The Marquise–Rinxent agglomeration (located in the south of landscape Section 11, see Fig. 1) provides high resistance to amphibian dispersal yet does not, in spite of its elongated shape, increase the modelled dispersal cost among adjacent *Alytes obstetricans* (triangle symbols) and *Triturus cristatus* populations (square symbols) by much. Corridors are shown by interrupted lines; links are as in Fig. 3

land of Section 11, but remained well-represented in the dune habitats of Section 7. A relatively low recording frequency for *Rana temporaria* may be due to its early breeding, in combination with newt predation on embryos and hatchlings (Denton and Beebee 1991).

Species of moderate occurrence

Epidalea calamita and *H. arborea* were found in the two dune areas and adjacent marshes along with several more or less distant occurrences inland. The marked decline of *E. calamita* in the Section 7 dune habitat may be caused by the regrowth of vegetation over open areas created by military activities in the Second World War. Indeed, the increase of grass and shrubs from the first to the third survey is substantial (see Fig. 1b and Appendix I in Supplementary materials). Clearing vegetation is a common practice in conservation management for *E. calamita* (Denton et al. 1997; McGrath and Lorenzen 2010; Buckley et al. 2014), and is likely to be required to restore populations in this area. The high frequency of *H. arborea* at persisting ponds (Table 1) is atypical (Schneider and Grosse 2009 and references therein). The decline of *H. arborea* was most pronounced in the agricultural land of Section 11, where three other species also declined significantly. Numerical declines may be more or less pronounced than shown by presence/absence data from ponds, and quantitative surveys are required, e.g., by counting egg-strings (*E. calamita*), or by recording the calls of displaying males (both species) to assess their current population status.

Rare species

Rana arvalis was observed in the first survey (see also Zuiderwijk 1980) and not later on. It would however be premature to declare the species locally extinct, because the marshes where we found it are popular for duck-hunting and access was frequently denied (more so in 2011 than in 1974). The species persists in the south of dpt. Pas-de-Calais and a

population was recently discovered in the Picardie region (Caby et al. 2000; Godin and Thiriet 2012). *Pelodytes punctatus* was found in three areas with remarkably different environmental characteristics, namely dunes (Section 7), quarries (Section 9) and agricultural land (Section 11). For reasons not understood, *P. kl. esculentus* is absent from the coastal zone, whereas more inland it is fairly common (Godin 2002). *Salamandra salamandra* larvae were found in standing water as well as in small streams, and the presence of the species at some coastal calcareous cliffs is notable (as in Thirion et al. 2014). Since the focus in our surveys was on standing water bodies, the occurrence of *S. salamandra* may have been underestimated.

Species in strong decline

Two species, *T. cristatus* and *A. obstetricans* stand out from the others on account of a sharp decline over more than one area (Tables 1, 2). The observations at the second survey suggest that the decline of *A. obstetricans* preceded that of *T. cristatus* (Appendix II in Supplementary materials). For both species the decline was concentrated in Sections 5, 9 and 11. *Alytes obstetricans* and *T. cristatus* share some of their aquatic habitat requirements (vegetated field ponds, drinking troughs) and it is presumably no coincidence that these species declined in similar fashion. However, a sharp decline of *A. obstetricans* (and not *T. cristatus*) was also observed at 46 persisting ponds (from 32 to 6%), suggesting threats additional to pond loss, such as fish introductions and disease. In particular *A. obstetricans* has been reported to decline under the influence of Chytridiomycosis and ranavirus (Bosch et al. 2001; Price et al. 2014; Rosa et al. 2013). However, the testing for the prevalence of disease organisms fell outside the scope of our study.

Population developments

Measured through the presence/absence of 13 species, the amphibian fauna studied has been remarkably stable, except for the severe decline shown by two species (*A. obstetricans* and *T. cristatus*) and the possible local extinction of *R. arvalis*. For the other species, the overall situation appears similar to that recorded by Crochet et al. (2004) for the south of France, where 56 ponds were surveyed with a ca. 30 yr interval without major declines, as far as detectable with presence/absence data. Current ‘hot-spots’ for the amphibians of the coastal zone of dpt. Pas-de-Calais are Sections 3 and 6, both of which are relatively small, pond-rich areas. These areas are currently under conservation management, where they were not at the time of the first survey.

Agricultural reform, amphibian dispersal and prospects for future research

It was only recently recognized that ponds and other small sized wetlands may make a significant contribution to the biodiversity of entire landscapes (Williams et al. 2003; Gioria et al. 2010; Ruggiero et al. 2008; Scheffer et al. 2006). However, due to their small size, ponds are prone to destruction and to increased isolation through structural changes in the surrounding landscape (Boothby 2003). The pond loss we recorded amounts to 3.5% per year (Curado et al. 2011). This is higher than in most other areas studied (e.g. Wood et al. 2003) but lower than what we observed in western France (Visser et al. 2017). Moreover, new ponds are also being created, making this a dynamic system.

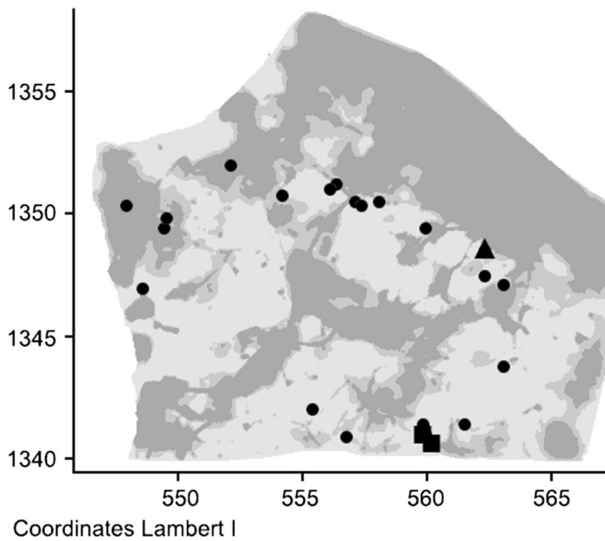


Fig. 7 The suitability of the landscape for pond creation, as determined from models of pond loss by in dpt. Pas-de-Calais, north-western France (Curado et al. 2011). *Dark shading* poor suitability, *medium shading* intermediate suitability and *light shading* good suitability. The *solid dots* indicate 22 ponds restored or newly created through the organization Parc Naturel Régional des Caps et Marais d’Opale Espace. A pond colonized by *Alytes obstetricans* is shown by a *triangle symbol* and two neighbouring ponds colonized by *Triturus cristatus* are shown by *square symbols*

The potential dispersal of pond breeding amphibians remains difficult to assess. In our analyses we made the principal decision not to rely on expert opinion to assess land-use induced resistance to dispersal but to use values derived from presence/absence data. Yet, it is worth noting that the resistance values that we determined are broadly similar to those suggested by experts (cf. Ray et al. 2002; Lenhardt et al. 2013). A consensus exists on the general negative influence of urbanization and arable cultivation (Greenwald et al. 2009; Riley et al. 2005; Trochet et al. 2016) and the heavy toll that roads inflict on amphibian populations is well documented (Fahrig and Rytwinski 2009; Garriga et al. 2012; Glista et al. 2008; Hartel et al. 2010; Rytwinski and Fahrig 2012).

Our results showed that informed and naïve dispersal routes were highly similar in terms of dispersal resistance, which we relate to the mosaic configuration of terrestrial habitats. The similarity between the modelled paths for either dispersal model (informed least-cost versus uninformed random motion) (Fig. 6; Table 3), is a point made previously by Balkenhol et al. (2009) (see also Janin et al. 2009; Cushman et al. 2013). Upon this analysis we decided that a careful evaluation of dispersal model appropriateness as advocated by Baguette and Van Dyck (2007) is not meaningful under the conditions we encountered. Rather we disregarded the ‘informed’ dispersal model because of the operating temporal and spatial scales.

Considering a lifetime maximum dispersal distance of 8–9 km for newts and salamanders and ca. 12 km for frogs and toads (Smith and Green 2005; Trochet et al. 2014) the two (coastal and inland) locations of *S. salamandra* and *P. punctatus* can be considered as separate ‘closed populations’ (Sinsch 2014). However, most species in our study are ‘panmictic patchy populations, with broad gene flow among neighbouring patches’, as evidenced by the colonization of newly created ponds (Appendix II in Supplementary

materials). *Alytes obstetricans* and *T. cristatus* fell into this category at the first survey, but the decline revealed by our study indicates that are currently better classified as ‘metapopulations ... consisting of several interacting local populations with occasional gene flow and local extinction and colonization dynamics’ (Fig. 3). The acid test for metapopulation coherence will be the natural colonization of newly created ponds over longer distances, such as those created in our study area by the Parc Naturel Régional (Fig. 7). On the basis of our assumption that good habitat to live in is good habitat to disperse through, our prediction is that new ponds in the southern agricultural land will more rapidly be colonized than those in the northern agricultural land. This can easily be determined in the field on the basis of their mating calls (*A. obstetricans*) and easy-to-spot eggs (*T. cristatus*), with near-unity detection probabilities so that solid inventories can be made (cf. Naujokaitis-Lewis et al. 2013). Testable models can be built on the basis of land use maps and the documented dispersal capacities of the species (Laan and Verboom 1990; Arntzen and Wallis 1991) along with genetic assignment tests that allocate individuals in a new pond to their population of origin.

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Author contributions The project was designed by JWA and AZ, fieldwork was carried out by AZ, JWA, CA and WRMM, analyses were done by JWA, RI and WRMM and the manuscript was prepared by JWA with the input of all authors.

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